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ON THE LIMITS OF THE CLASS OF FISHES.

BY THEODORE GILL, M.D., PH.D.

IN the classification of the animal kingdom the vague ideas prevalent among the vulgar and originating in prejudices based on habitat or external appearance have been more or less reflected, and special forms associated with earth, air and water. Thus were the inhabitants of the "element" associated together on the one hand, and separated from those of other "elements" in the other by the ancient cosmologists and poets.* This was the first generalization or attempt to combine the groups which from all time have been recognized as "beasts" or "animals," "birds," "fishes," and others in still more comprehensive groups. But, in time, and as investigation was directed to the structure of animals, it was found that the preconceived ideas respecting the relations of the various forms to the media which they inhabited, were by no means the correct expressions of the relations of such forms in structural features. The recognition of this fact resulted in the admission of several classes (anticipating the definite ideas which are now associated with such groups) and the virtual separation of the vertebrates from the invertebrates. But the ancient

*In the beginning God created the *heaven* and the *earth*. And the earth was without form and void.

And God made the firmament, and divided the *waters* that were *under* the firmament, from the *waters* that were *above* the firmament: and it was so. And God said: Let the waters under the heaven be gathered together unto one place, and let the *dry land* appear: and it was so.

And God said: Let the *waters* bring forth abundantly the *moving creature* that hath life, and *fowl* that may fly above the earth, in the *open firmament* of heaven.

And God said: Let the *earth* bring forth the *living creature* after his kind, cattle and creeping thing, and beast of the earth after his kind: and it was so.—*Genesis, Ch. I, verses 1, 2, 7, 9, 20, 24.*

The same idea is expressed by several of the ancient poets and especially by Ovid in the following lines:—

Ante mare et tellus, et, quod tegit omnia, cælum,
Unus erat toto naturæ vultus in orbe,
Quem dixere Chaos; rudis indigestaque moles;
Hanc Deus et melior litem natura diremit:
Nam cælo terras, et terris abscidit undas;
Neu regio foret ulla suis animantibus orba;
Astra tenent cæleste solum, formæque deorum;
Cesserunt nitidis habitandæ piscibus undæ;
Terra feras cepit; volucres agitabilis ær.

— Ovid, *Met. I, l. 5–7, 21–22, 72–75.*

idea of a certain relation between form and habitat still prevailed to a greater or less extent, and the vertebrates, in the earliest days of systematic zoology, were instinctively divided into quadrupeds, or animals especially fitted for progression on land; birds, especially adapted for flight and fishes, destined for life in the waters; while those animals not referable to either category, such as reptiles, bats, etc., were slurred over or forced into combination with the others on account of some points of real or supposed agreement. Soon, however, the distinction of the cold-blooded quadrupeds from the warm-blooded ones (mammals) and the affinity of the former and the serpents were recognized, and the class of "reptiles" constituted. It was long before it was fully and generally acknowledged that the latter was a heterogeneous assemblage of forms having very diverse relations, part of them being closely related to birds, and the others almost undistinguishable from fishes. Such recognition has now become practically universal, but, at this point, the progress of zoological taxonomy as exhibited in the appreciation of the subordination of types has been to a great extent arrested, and naturalists have mostly been content to recognize the five classes, Mammals, Birds, Reptiles, Batrachians, and Fishes. Several naturalists, however, have dissented from this view, and indeed the class of fishes has not been so universally recognized with the limits the mind is still most apt to connect with it as is usually supposed.

The Class and its modifications.—The cetaceans and fishes were regarded as a group coördinate with the warm-blooded quadrupeds (mammals) and birds, either avowedly or by implication, till Brisson, in 1760, finally withdrew the former from the class, and placed them in more immediate relation with the warm-blooded quadrupeds, regarding them, however, as constituting a peculiar class: the class of fishes, thus relieved, was for the first time presented with the limits since generally recognized.

It is true that, as a matter of fact, the agreement of the cetaceans with the mammals in their respiratory apparatus and warm blood had been long previously recognized, even by Aristotle and indeed by every observer capable of comparison of facts, but in spite of such recognition, the apparent agreement in form and adaptability for progression in the waters exercised such a preponderant influence over the mind, that the hints thus offered were not accepted in their fulness till 1758 by Linné.

Linné first, in the tenth edition of his "*Systema Naturæ*" (1758), eliminated the cetaceans from the class of fishes and combined them with the viviparous quadrupeds in a single class, for which he proposed the now universally accepted name *Mammalia*. At the same time that he eliminated the cetaceans, however, he violently divorced from the class of fishes and referred to the *Amphibia*, under the name *Amphibia nantes*, first (in 1758), all the *Chondropterygii* of Artedi (except the sturgeons) as well as the genus *Lophius*; and, subsequently (1766), he removed still others from the class, completing the removal of the *Chondropterygii* by the exclusion of the sturgeons, and discharging at the same time the genera *Cyclopterus*, *Balistes*, *Ostracion*, *Tetrodon*, *Diodon*, *Centriscus*, *Syngnathus* and *Pegasus*, most of which formed the *Branchiostegi* of Artedi. He seems to have been led to this measure by the belief that they were provided with lungs instead of gills, apparently having been misled by an erroneous observation of Dr. Garden, of Charleston, on *Tetrodon*.

Gmelin, in his edition of the "*Systema Naturæ*" (1788), restored to the class the forms thus divorced from the fishes.

The genus *Myxine* was referred to the class *Vermes* by Linné and his followers, and therefore doubtless was overlooked by Bloch, who redescribed it as a fish under the name *Gastrobranchus*.

The constituents of the class having been at length, for the time, agreed upon, the question of its subdivision or union with others was next agitated.

Pallas combined the fishes with the *Amphibia* of Linné in a class, coördinate with mammals and birds, which he named *Monocardia*. Long afterwards, Prof. Owen adopted the same view, but gave the new name *Hæmatoecrya*.

On the other hand, the elder Geoffroy St.-Hilaire, and following him, Latreille,* separated the combined *Elasmobranchiates* and *Marsipobranchiates* as a class (equivalent to the order *Spiraculata* of Pallas), and named it *Ichthyoderes* or *Ichthyodera*. This view, however, fell still-born.

In 1856, Prince Charles Bonaparte† recalled that Isidore Geof-

* LATREILLE (Pierre André)—*Familles Naturelles du Règne Animal, exposées succinctement et dans un ordre analytique avec l'indication de leurs genres*. Paris, J. B. Baillière. Libraire de Bandonin Frères. 1825. [8vo, 570 pp.]—Troisième Classe, *Ichthyodères*, *Ichthyodera* (G. St. H.), p. 107; Quatrième Classe, *Poissons*, *Pisces*. p. 112.

† Bonaparte (Prince Charles Lucien) *Additions et corrections aux Tableaux paralléliques de la deuxième sous-classe des Oiseaux, Précoces ou Autophages*; . . .

froy St.-Hilaire* had, in 1852, separated from the class of fishes as the type of a new class (Myelozoa) the genus Branchiostoma or Amphioxus (a species which was originally described by Pallas as a member of the molluscan genus Limax), rediscovered and first referred to the class of fishes by Costa in 1834. Bonaparte, at the same time, proposed to withdraw from the invertebrates the genus Sagitta (Quoy and Gaimard) and elevate it to the rank of a class (Aphanozoa) of the vertebrates.†

In the elevation of Sagitta to the rank of a class Bonaparte has anticipated Professors Carus and Huxley (who also elevated the same form to class rank, retaining the name Chætognatha, originally conferred upon it as the type of an *order* by Leuckart). But his views respecting its pertinence to the branch of vertebrates are untenable, for there can now be no doubt that it is at least most nearly related to the class of annelides.

In 1857, the question of the primary classification of fishes was again reviewed by Prof. Agassiz. That eminent zoologist "was satisfied that the differences which exist between the Selachians (the skates, sharks, and Chimærae) are of the same kind as those which distinguish the amphibians from the reptiles proper and justify, therefore, their separation, as a class, from the fishes proper. I consider also (he adds) the Cyclostomes as a distinct class for similar reasons; but I am still doubtful whether the Ganoids should be separated also from the ordinary fishes." He finally however admitted four classes, viz :—

"1st class; Myzontes with two orders, Myxinoids and Cyclostomes.

(Suite et fin.) <Comptes rendus hebdomadaires des séances de l'Académie des Sciences, (1er Dec. 1856) XLIII, 1017-1027.

* I have been unable to find any memoir or paragraph in any work by Geoffroy St.-Hilaire embodying the view referred to, and suspect it may have been a verbal communication, and never actually published.

† Que le Sagitta, Quoy et Gaimard, cet animal singulier si commun dans les mers du Nord, découvert par nos intrépides voyageurs, et ballotté par les savants entre les Mollusques, les Vers et jusqu'aux Acalèphes! possède dans la première période de sa vie une grosse corde dorsale qui en fait un Vertébré subissant une métamorphose rétrograde dans le sens de Rathke. C'est à M. Meissner, jeune professeur à Bâle, qu'on doit cette belle découverte. Cet animal, qui dans l'état actuel de la science ne pourrait être regardé que comme un Poisson, pour ainsi dire, dégradé, mériterait de former une classe à part, bien plus encore que l'Amphioxus ou Branchiostoma, dont notre savant Président a fait le type de sa classe des *Myélaires* (Myelozoa), depuis 1852.

En effet, la corde dorsale (qui forme le distinctif essentiel des Vertébrés) s'oblitérant et disparaissant complètement dans l'adulte, constitue un caractère tellement important, qu'il ne peut désigner un groupe d'un rang moins élevé que celui de classe; il pourrait être convenable de donner à cette classe le nom d'*Aphaniaires* ou Aphanozoa. *Op. cit.* p. 1022.

2d class ; Fishes proper with two orders, Ctenoids and Cycloids.

3d class ; Ganoids with three orders, Coelacanth, Acipenseroids, and Sauroids ; and, doubtful, the Siluroids, Plectognaths and Lophobranchs.

4th class ; Selachians with their orders, Chimærae, Galeodes, and Batides.*

The Leptocardians and Dipnoans were not referred to in this essay and consequently it is doubtful what the author considered to be their relations.

In 1866, Prof. Hæckel also divided the fishes into four classes, but on entirely different grounds and with extremely different limits from those proposed by Prof. Agassiz ; the classes recognized by Hæckel being represented severally by (1) Branchiostoma (Leptocardia), (2) the Myxinoids and Petromyzontes (Cyclostoma) and (3) all other fishes (Pisces) except Protoptera, which (4) constitutes a fourth class (Dipneusta). Hæckel, moreover, does not consider the fishes as a group coördinate with any combination of other vertebrate classes ; contrasting the Leptocardia in a group (Subphylum Leptocardia or Acrania) opposed to all the rest of the vertebrates (Subphylum Pachycardia or Craniota) ; and under the latter opposing the (1) Cyclostoma in a "cladus" or superclass Hauptklasse Monorrhina, coördinate with (2) another (Anamnia) containing the fishes, "Dipneusta," "Halisauria" (extinct swimming reptiles), and Batrachians, and (3) a third (Amniota) embracing reptiles, birds and mammals.†

In 1868, Prof. Cope,‡ in a suggestive article on the doctrine of evolution, considered the Leptocardii, Dermopteri, Elasmobranchii, Teleostei (including Ganoidei as a subclass) and Dipnoi to be groups coördinate with the Batrachia, Reptilia, Aves and Mammalia and therefore classes :§ in a subsequent memoir, he reiterates more distinctly the same opinion, remarking that "The *classes* Aves, Reptilia, and Batrachia are those over which the present review extends. The *classes* of vertebrata not included are : the

* Agassiz (Louis). Contributions to the Natural History of the United States of America, I, 1857, p. 187 (= Essay on classification, chap. iii, section i).

† Hæckel (Ernst). Generelle Morphologie der Organismen, b. 2 (Allgemeine Entwicklungsgeschichte der Organismen), 1866, pp. cxviii-cxxix ; also *ib.* Natürliche Schöpfungsgeschichte (1868), 2e. Aufl. 1870, pp. 512-513, etc.

‡ COPE (Edward Drinker). On the Origin of Genera . . . < Proceedings of the Academy of Natural Sciences of Philadelphia, 1868, p. 256-265.

§ The groups in question are arranged in the same vertical line in five tables exhibiting anatomical details in which the subordination of groups appears to have been carefully considered and attempted to be represented.

Dipnoi, Pisces, Elasmobranchii, Dermopteri, Leptocardii and the Mammalia.*

Subsequently, in a most important special memoir on the classification of fishes, Prof. Cope † (if I understand his views) recognized (as classes) six groups of Vertebrata; Mammalia, Sauropsida (birds and reptiles), Batrachia, Pisces, Dermopteri, and Leptocardii. After enumerating these groups, he adds: "These six *classes* of Vertebrata appear to be well established."

Three classes among Fishes.—After a careful survey of the field, the author had independently, several years ago, arrived at the same conclusion as Prof. Cope respecting the old class of fishes, but had neglected to announce them except in conversation with others engaged in like pursuit, and in lectures. He had, however, somewhat inclined to the recognition of the Elasmobranchiates as a class, but considers such at present inadvisable and perhaps uncalled for by the evidence; like Prof. Cope, he cannot agree with Prof. Hæckel in the separation of the Dipnoans from the class Pisces, the relations of that form with Polypterus and other universally recognized Ganoids being more intimate than those between such Ganoids and the typical fishes. The number of classes recognized as confounded under the common designation of fishes will then be three, viz :—

I. PISCES.

SYNONYMES, AS CLASSES.

- < Pisces, *Artedi*, 1738, Linné, 1735-1754 (incl. Cete).
- > Pisces, *Linné*, 1756, etc. (excl. *Chondropterygii*, etc.)
- > Poissons (Pisces), *Geoff. St. Hilaire, Latreille*, 1825.
- > Ichthyoderes (Ichthyodera), *Geoff. St. Hilaire, Latreille*, 1825.
- > Fishes proper, *Agass.*, 1857.
- > Ganoids, *Agass.*, 1857.
- > Selachians, *Agass.*, 1857.
- > Pisces, *Hæckel*, 1866.
- > Dipneusta, *Hæckel*, 1866.
- > Dipnoi, *Cope*, 1868.
- > Teleostei, *Cope*, 1868.
- > Elasmobranchii, *Cope*, 1868.
- = Pisces, *Cope*, 1872.
- Fishes part., *auct. plur.*

* COPE (E. D.) Synopsis of the extinct Batrachia and Reptilia of North America, 1869, p. 3; Trans. Am. Phil. Soc., v, 14, p. 3.

† Cope (Edward Drinker). Observations on the Systematic Relations of the Fishes. (Contributions to the Ichthyology of the Lesser Antilles, §I.) < Transactions of the American Philosophical Society (Philadelphia), 2d series, v. 14, pp. 447, 1872.

The same memoir with the same title is printed in the American Naturalist for September, 1871 (vol. 5, pp. 579-593, and in the Proceedings of the American Association for the Advancement of Science, 1871, (1872) pp. 317-343, but without the paragraph cited.

II. MARSIPOBRANCHIATES.

SYNONYMES, AS CLASSES.

- <Ichthyoderes (Ichthyodera), *Geoff. St. Hilaire, Latreille*, 1825.
 <Myzontes, *Agass.*, 1857 (including *Amphioxus*?).
 =Cyclostoma, *Hüchel*, 1856.
 =Dermopteri, *Cope*, 1868, 1872.

SYNONYMES, AS SUBCLASS.

- = Marsipobranchii, *Bon.*, 1810 (incl. Leptocardii).
 = " Müller, 1844 *et auct. plur.*
 < " Bon., 1846.
 <Dermopteri, *Gill*, 1861, *Owen*, 1853.

III. LEPTOCARDIANS.

SYNONYMES, AS CLASS.

- = Myelozoa, *Is. Geoff. St. Hil.*, *Bon.*, 1856.
 <Myzontes, *Agass.*, 1857.
 = Leptocardia, *Hüchel*, 1856.
 = Leptocardii, *Cope*, 1868, 1872.

SYNONYMES, AS SUBCLASS.

- = Leptocardii, *Müller*, 1844, *et auct. plur.*
 <Dermopteri, *Gill*, 1861, *Owen*, 1853.

These three classes appear to be better entitled to such distinction than any of the higher classes of vertebrates, both on account of the greater taxonomic value of their distinctive characters, and their isolation from the next allied forms; and in both these respects, they are, for example, far more worthy of recognition than the classes of birds and reptiles as distinguished from each other, or the Pisces on the one hand and the Batrachians on the other. The difficulty, indeed, in the case of the inferior classes consists not in the inability to distinguish them from each other, but in the task of tracing the homologies between them, and there is no evident reason why this state of facts should not be to some extent reflected in the classification. The chief objection thereto of which the author is aware is a current and vague idea that what are called lower forms are more elastic and exhibit a wider range of variation than superior ones, and by *assuming* that all low forms of any branch, however much they may differ in structure, are constituents of a natural group to be compared with several more restricted higher ones; such views may be enforced, but are liable to be considered, and only worthy of being treated, as *petitiones principii*.

Certainly, the differences between Branchiostoma (*Amphioxus*) and its nearest of kin are as evident and striking as those between

any contiguous classes in the entire animal kingdom ;* that, furthermore, they are significant of the highest class taxonomic value is indicated by their fundamental nature, and the coördination of all parts of the organization.

There is also no longer reason for hesitancy in the admission of such a rank on the plea of imperfect knowledge of structure or the supposition that it may be the young of some other form †—a suspicion formerly common to many and shared by the author. With these facts, therefore, something more than mere assertion of opinion is requisite before the title of the group to at least class rank can be questioned.

A much mooted question has been what are the characters of the class of fishes, and how are they distinguished from the class of batrachians. This question has been discussed by Dr. Brandt, of St. Petersburg, in an elaborate memoir.‡ So long as the fishes, Marsipobranchiates and Leptocardians, were confounded in one class, the extreme variations of the so-called class blinded one to the minor differences that would otherwise have been seized, and the result was that no absolute characters were discovered to limit the so-called class. But the class purged of the Marsipobranchiates and Leptocardians offers no longer such obstacles, and although the characters appear to have been overlooked hitherto, it is not the less true that all the known fishes are absolutely distinguished from all the known batrachians by very

* PARKER (William Kitchen), "On the Structure and Development of the Skull of the Common Frog (*Rana temporaria* L." [Phil. Tr. 1871, p. 202-3], well remarks "The lowest existing fish but one is the Myxinoid (lamprey, hag, *Bdellostoma*); between it and the lowest vertebrate, the lancelet (*Amphioxus*), there is a gap, the extent of which has never been imagined; and yet even the lancelet itself is not necessarily the boundary form. . . . Every anatomist will at once see that a creature no higher in type than the unhatched embryo of the frog is yet an untold distance in advance of the lancelet which yet is only the *known lowest* of the great vertebrate subkingdom.

† BERT (P.) Sur l'Amphioxus. Note de M. P. Bert. . . . <Comptes rendus hebdomadaires des séances de l'Académie des Sciences (Paris), t. 65, 1871, pp. 364-7; translated (On the anatomy and physiology of *Amphioxus*) <The Annals and Magazine of Natural History, third series, 20, 1867, pp. 302. Contains notes on the ejection of semen, etc.

KOWALEVSKY (A.) Entwicklungsgeschichte des *Amphioxus lanceolatus*. . . . 1867. [4to. 1 pl., 17 pp. 3 pl.] <Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg, viie Série, t. xi, no. 4.

An account of the development of the species. The eggs are expelled through the mouth.

‡ BRANDT (Johann Friedrich). Bemerkungen über die Classification der Kaltblütigen Rückenmarkthiere zur Beantwortung der Frage Was ist ein Fisch? . . . St. Petersburg, 1865 [4to. 1 pl., 30 pp.] = Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg, 7e série, t. 9, no. 3.

obvious ones. All the batrachians have a scapula (in the broadest sense) which is homogeneous, the only differentiation being in the simple ossification of parts and which is always confined to the side; on the other hand, in all the fishes the shoulder girdle has somewhat the form of the furcula (wish-bone) of a bird, and really forms a girdle behind the head, inclining forward and connected below, either by a median cartilage or directly, and a wholly differentiated element (answering to the paraglenal or coracoid* region of Batrachians), or elements, support the pectoral member. The Dipnoans (*Lepidosiren*, etc.) and all other fishes agree in this respect and differ from the Batrachians.

In conclusion the following analytical synopsis (extracted from the author's "Arrangement of the Families of Fishes," published by the Smithsonian Institution) will exhibit the principal characters which distinguish the several classes confounded under the name of Fishes. The characters used are supplemented by many others:—

CLASSES.

I. Skull more or less developed, with the notochord not continued forwards beyond the pituitary body. Brain differentiated and distinctly developed. Heart developed and divided at least into an auricle and ventricle.

A. Skull well developed, and with a lower jaw. Paired fins developed (sometimes absent through atrophy); and with a shoulder girdle (lyriform or furcula-shaped, curved forwards and with its respective sides connected below†), and with pelvic elements. Gills not purse-shaped. PISCES.

B. Skull imperfectly developed and with no lower jaw. Paired fins undeveloped, with no shoulder girdle nor pelvic elements. Gills purse-shaped. MARSIPOBRANCHII.

II. Skull undeveloped, with the notochord persistent and extending to the anterior end of the head. Brain not distinctly differentiated. Heart none. LEPTOCARDII.

*This is generally multiple, and its elements have been identified with the radius, ulna, and humerus (Owen = third bone of the fore-arm of Cuvier). In a special article, I have discussed these homologies.

†The shoulder girdle of the Elasmobranchiates appears to be homologous with the paraglenal or coracoid elements of the specialized fishes, the proscapula of the latter having been apparently first developed by exostosis in the Ganoids, and finally become preponderant while the Paraglenal became proportionately reduced.